# Composition and Structure of Lowland Rain-Forest Tree Communities on Ta'u, American Samoa[1]

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**Abstract:** This study examined the composition and structure of tropical rain forest in four permanent plots on the island of Ta'u, American Samoa. Two 1-ha plots were established in coastal forest, one in an abandoned coastal cultivation site (a "plantation" ca. 17 yr post-abandonment) and another in a *Dysoxylum samoense*–dominated coastal forest. Two 2-ha plots were established in lowland forest at 200–250 m elevation, one in an abandoned plantation (ca. 13 yr post-abandonment) and the other in less-disturbed mid- to late-secondary mixed lowland forest. In the total 6 ha, we encountered 54 tree species, with *Dysoxylum samoense* the most dominant species overall and abundant in all four plots. The upper forest plot was the most diverse plot and exhibited low similarity with any of the other three plots. This plot exhibited a rarefaction curve similar to those of four lowland hill forest plots on Tutuila but was most similar in composition to regenerating disturbed forest on Tutuila rather than mature, less-disturbed forest. Low similarity was found between the two *Dysoxylum*-dominated coastal forests and the *Dysoxylum-Pometia*–dominated Ottoville lava flow forest on Tutuila. By examining the populations of *D. samoense* across the four plots we found an impact of agriculture and cyclones on height structure of the forest. Examination of species' diameter class distributions allowed us to propose several hypotheses related to the life histories of several tree species. We documented the natural establishment of the introduced species *Flueggea flexuosa* into both abandoned plantations and natural forest. Monitoring these plots over time will allow us to better understand successional processes in natural and human-impacted forest including changes in composition, structure, relative abundance of nonnative species, as well as the impact of cyclones on different forest types.

FOREST COVERS MORE than half the surface of the five main islands of American Samoa. Lowland rain forest, occurring from sea level to 350–500 m elevation, is the most widespread forest type on the Islands, differentiated into several habitat types including coastal, ridge, valley, slope, and lava flow forests (Whistler 2002). These habitat types are a function of topographical position (Webb et al. 1999), with the exception of lava flow forest, which is formed on relatively flat, young lava flows (Whistler 1980, 2002).

The island of Ta'u is located approximately 100 km east of Tutuila, at 169° 28′ W, 14° 14′ S. It is a small (39 km$^2$) shield volcano formed over a geologic hot spot that formed the entire Samoan Archipelago. Ta'u is the youngest of the high islands of the Samoan Island chain, being formed approximately 300,000 yr B.P. (Nunn 1998). Although the island of Ta'u was formed by the

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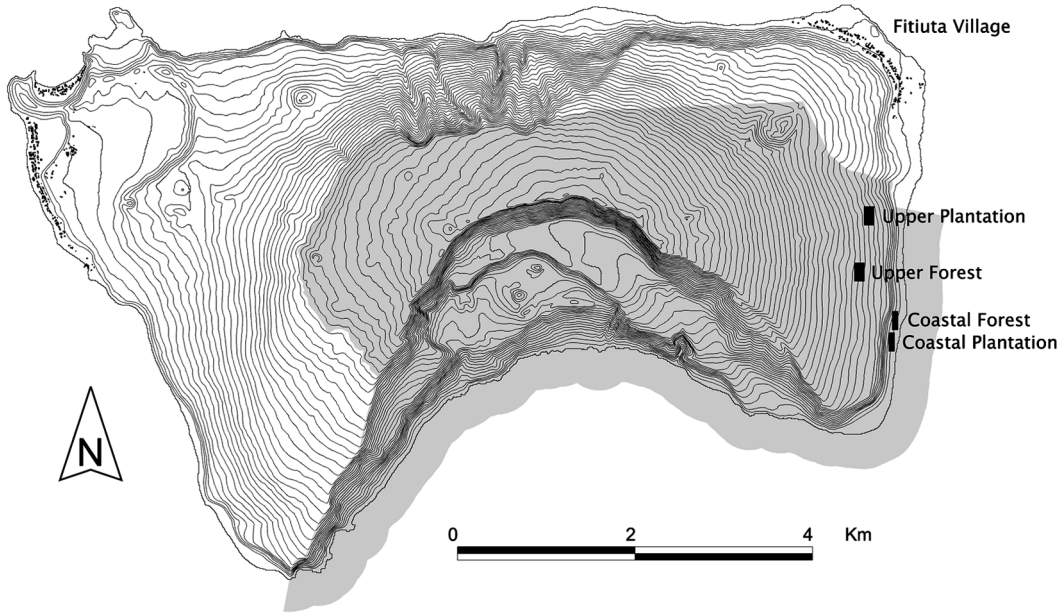


FIGURE 1. Topographic map of Ta'u showing location of the four plots in this study. The shaded area represents the National Park of American Samoa. Contours are 20-m elevation intervals.

activity of one large volcano (Lata Volcano), two smaller lava volcanoes, Tunoa Volcano and Luatele Volcano, contributed lava flows to the northwestern and northeastern corners of the island. On the south side of the island, steep cliffs from Lata summit (960 m above sea level) to the sea are the inner walls of the caldera exposed as a result of the collapse of the southern half of the island (Figure 1).

The forests on Ta'u have been explored botanically since the early 1800s. Whistler (1992) estimated that the native vascular flora of Ta'u was 329 species, which is about 60% of the estimated 550 native vascular species of the Samoan Archipelago (Whistler 1992). In addition, there are approximately 131 introduced species on Ta'u. Botanical data have allowed researchers to propose forest classifications, with lowland rain forest accounting for the majority of American Samoan forest (Amerson et al. 1982a,b). Lowland rain forest can be subdivided further into assemblages based on the dominant canopy tree species (Mueller-Dombois and Fosberg 1998).

Whistler (1980, 1992) differentiated lowland forest of Ta'u into several habitat types, including littoral forest, *Dysoxylum* lowland forest, mixed lowland forest, and secondary forest. Secondary forest refers to forest recovering from either natural or human-induced disturbances. Because humans have inhabited and cultivated Ta'u for ca. 3,000 yr (Hunt and Kirch 1997) and hurricane disturbance is a frequent occurrence in the Samoan Archipelago (Elmqvist et al. 1994), most of the forests of Ta'u (and Samoa in general) are in some stage of recovery.

Despite extensive research on the botany of American Samoa, limited research has been undertaken on forest dynamics. Elmqvist et al. (1994, 2001) and Hjerpe et al. (2001) investigated the impacts of cyclones on forest structure on Savai'i, Samoa. Whistler (1980, 1995) established several small (1,000 $m^2$ each) permanent forest plots in American Samoa for long-term monitoring.

Webb and Fa'aumu (1999) established a set of 1.2-ha permanent forest plots on Tutuila to monitor the dynamics of tree communities. In this study, we established a set of permanent forest plots on the island of Ta'u, American Samoa, for long-term monitoring of forest dynamics. Here we report the composition and structure of tree communities in coastal and upland forest on Ta'u. Current structure and composition of Samoan forest reflect past disturbance history as well as other inherent geophysical and biological factors (Whistler 1980, Webb and Fa'aumu 1999, Webb et al. 1999), and we expected to find differences in our plots that reflected historical disturbance as well as elevational (i.e., locational) differences.

## MATERIALS AND METHODS

### *Site Overview*

This research took place in the 29-km$^2$ Ta'u unit of the National Park of American Samoa (Figure 1). Reconnaissance hikes were taken to acquire a general understanding of the forest structure and composition of Ta'u forests before deciding on final plot locations. We also interviewed key informants in the village of Fitiuta, which holds customary use rights over the eastern portion of Ta'u. These interviews provided a general history of forest use and an anthropological framework within which to study forest conditions. Subsequent to the preliminary reconnaissance hikes and general survey, we selected four sites to establish permanent plots.

Across the eastern coastline of Ta'u, a flat bed of basaltic alluvium and coral rubble extends from the high tide line inland for about 150 m, where a steep escarpment rises to about 170 m. Soil of this narrow strip of land has been characterized as a Typic Ustipsamment, an extremely cobbly and sandy Ngedebus variant formed in water and wind-deposited coral sand (Natural Resources Conservation Service 2004). It is a deep and very well-drained soil. Above the escarpment up to about 275–300 m asl, the soils are variants of the Pavaiai Series, which are moderately deep, well-drained, stony clay loams (Typic Dystrandepts) formed in volcanic ash and underlain with lava (Natural Resources Conservation Service 2004). The topography above the escarpment is gently sloping (approximately 12° according to topographic data) and not highly dissected by streams. Some of the area had been terraced to facilitate agricultural practices in the past.

The 30-yr rainfall average on the island of Tutuila, 100 km to the west, is 3,022 mm and ranged from 1,398 to 3,335 mm between 1995 and 2004 (data from National Climatic Data Center, National Oceanographic and Atmospheric Administration). There were no precipitation data available for Ta'u, so the numbers from Tutuila can only serve as an approximate guide.

The forests of Ta'u, like virtually all of Samoa, are managed under a traditional clan-ownership system (Elmqvist 2000). Before the establishment of the national park, the east side of Ta'u had been under cyclical cultivation and dispersed habitation for an unknown number of generations. According to our interviews, in areas where cultivation took place (referred to locally as a plantation), forest trees were cut or burned to reduce competition with short-term crops, such as taro (*Colocasia esculenta* (L.) Schott) and ta'amu (*Alocasia macrorhiza* Schott), and long-term crops such as breadfruit (*Artocarpus altilis* (Parkinson) Fosberg) and coconut (*Cocos nucifera* L.). Generally, attempts to remove all forest trees were not completely successful and some large trees could remain on farming land. After a few cropping cycles soil fertility declined, and the taro-ta'amu cropping was shifted to a new location.

Certain areas of the forests above the eastern escarpment of Ta'u were under cultivation in 1987 when cyclone Tusi passed and imparted severe damage to both forests and plantations. According to local residents, Tusi was a major cyclone that struck the eastern side of Ta'u, with strong winds from opposing directions as it passed. Plantations above the escarpment were abandoned after Tusi. Along the coast, plantations were still being utilized until about 1991, when cyclones Ofa

and Val struck the Samoan Archipelago. Coincidentally, the National Park of American Samoa was established and by 1992 all agricultural activity ceased in the area that is now the national park. No quantitative assessment was made of the damage to Ta'u forests caused by any of those cyclones.

We were able to ascertain the general agricultural and agroforestry practices on Ta'u and the history of the accessible coastal forest, but it was not possible to obtain information on the precise boundaries or land use histories (e.g., rotational period of crops) of clan-owned forests above the escarpment. Our categorization of plots as "forest" or "plantation" in this study was based on our understanding of the intensity of use through interviews. The plantation plots were recognized by village respondents as areas where large trees were removed for intensive cultivation, and forest plots were areas where canopy trees were not removed (indicating reduced impact on soils and maintenance of at least a partial canopy) or where respondents could not recall a plantation being there in their lifetime. This was supported by our field observations of the dominant species and forest structure at each site. Given the frequent occurrence of hurricanes in Samoa (Elmqvist et al. 1994) and in the South Pacific in general (Revell 1981, Mueller-Dombois and Fosberg 1998 [both cited in Franklin et al. 2004]), it is more accurate to consider the forest plots as mid- to late-successional forests rather than mature forests.

### *Data Collection and Analysis*

We established two 1-ha plots in coastal forest, and two 2-ha plots in slope forest above the escarpment adjacent to the eastern coastline (Figure 1). Plot sizes were smaller in the coastal zone because of limited availability of less-disturbed coastal forest. The first coastal plot (hereafter "coastal plantation") had been a coconut, taro, banana, and breadfruit plantation that, according to our interviews, was abandoned in about 1991–1992. Before conversion the site had been dominated by *Dysoxylum samoense*. We could not ascertain how long ago the site had been cleared, but we assumed it was several generations. This plot had a few large forest trees but abundant populations of *C. nucifera* and *A. altilis*.

A second plot (hereafter "coastal forest") was in forest described by Whistler (1980, 1992) as a *Dysoxylum* lowland forest. This patch of forest had a tall, continuous canopy dominated by *Dysoxylum samoense*, with other native forest trees in the understory. The bird's-nest fern, *Asplenium nidus*, was abundant on the forest floor and on rocks. The coastal forest plot encompassed the original 1,000-$m^2$ "Saua" plot of Whistler (1995), but we did not incorporate the earlier data into this study because we could not determine the previous diameter measurement point on each tree. The soil of both plots was the Ngedebus variant (i.e., poorly weathered basaltic alluvium with coral rubble).

A 2-ha plot was established at 200 m elevation in an area that according to our interviews was under heavy cultivation until about 1987 (hereafter "upper plantation"). The landscape had been terraced to facilitate cultivation. At the time of our survey, this forest was dominated by a robust and regenerating *A. altilis* population that had taken over the previous agricultural land. Although native forest trees and regeneration were encountered during our initial reconnaissance, it was clear that this site was dominated by the agroforestry species.

A 2-ha forest plot (hereafter "upper forest") was established at approximately 220–250 m elevation in forest we considered to reflect low to no disturbance from agriculture. Our interviews with local people indicated that this plot was in an area traditionally used for nonagricultural purposes (e.g., hunting Pacific pigeons [*Ducula pacifica*]). We found the site to be dominated by native tree species, with little or no representation of plantation species in the immediate vicinity. Moreover, there was a robust epiphyte load on many trees. These features indicated that the upper forest plot was much less disturbed by human activity than the upper plantation plot. The soil of the upper plots was the Pavaiai series.

We established the plots using standard

protocols for permanent forest plots around the world (Alder and Synnott 1992, Dallmeier and Comisky 1998). We used a sighting compass (Suunto KB-14) (accuracy 0.17 degree), laser distance meter (Leica DISTO) (accuracy $\pm 3$ mm), and PVC (polyvinyl chloride) tubes to mark the plots at 10-m intervals. We corrected for slope of the terrain using a clinometer (Suunto) and calculating the ground distance between each PVC tube required for a 10-m horizontal distance.

In each plot, we surveyed every stem $\geq 10$ cm dbh (diameter at breast height [1.4 m], avoiding stem irregularities), identified them to species, measured for dbh, and calculated the height using the clinometer. For trees that branched below 1.4 m height and for coppiced trees, we measured, tagged, and recorded each stem individually; however, the stems were all recorded as belonging to the same individual. A unique numbered tag was nailed to the stem 20 cm above the dbh measuring point. A map of all individuals, with multiple-stemmed trees being mapped only once, was created.

*Hibiscus tiliaceus* posed a particular challenge because it is a scrambling shrub or tree, and stems can set root in more than one location along a horizontal axis, producing multiple, potentially independent, clones. When we encountered rooting of *H. tiliaceus* beyond 1.4 m from the original base of the tree that would allow the new clone to survive in the case of damage to the main base, we considered each clone to be a unique individual. Any established adventitious roots within 1.4 m of the base of the tree were considered to be part of the main trunk. Using this rule allowed us to make consistent decisions for our data collection. However, it should be recognized that our definition of a *H. tiliaceus* individual does not necessarily imply that it is a genetically unique individual. This caveat applies only to *H. tiliaceus* and not to any other species in the plots. Our decision rule probably resulted in occasional redundancy in measurements of the same genets, but it is very unlikely that the overall results were affected.

We calculated diversity indices and tree densities based on the numbers of individuals. Population size-class distributions and basal area (the spatial area covered by stem cross section) calculations, however, included all stems. The importance value for each species was calculated as the sum of the relative abundance and the relative basal area. We did not include relative frequency in the calculation because subplots were not independent sampling units. Diversity indices, including richness, rarefaction curves, Simpson's $\lambda$ (Simpson 1949), and the modified Hill Ratio for evenness (Alatalo 1981), were calculated with the BASIC programs written by Ludwig and Reynolds (1988). The similarity among plot species compositions was calculated using the Morisita-Horn Index of similarity, which emphasizes relative abundances and was appropriate for our data set because it is less influenced by species richness and sample size than other similarity indices such as the Jaccard Index or Sorenson Index (Magurran 1988). We correlated stem density and basal area measurements using correlation and partial correlation, and compared the height of the tree canopy across plots (defined as the median height of the tallest 10% of trees in each plot) using a Kruskal-Wallis analysis of variance (ANOVA).

Some of the results presented here were compared with forest data from Tutuila Island. Four 1.2-ha permanent plots were established by Webb and Fa'aumu (1999) in lowland forest on steep slopes, one of which (Alava) was a regenerating cultivation site that had been abandoned approximately 30–40 yr prior and was more susceptible to cyclone damage than other plots due to its exposure. The other three plots (Amalau, Maloata, Vatia) had been less disturbed by humans. Alava, Maloata, and Vatia had clay soils with rocky outcrops, and Amalau had a very stony "talus" clay loam (Webb and Fa'aumu 1999). Seamon et al. (2006) surveyed approximately 3.1 ha of a lava flow forest dominated by *Pometia pinnata*, *Dysoxylum maota*, and *Dysoxylum samoense* in the Ottoville Lowland Forest on the Tafuna Plain, Tutuila. This forest was on very stony clay soil underlain with lava and exhibited substantial floral uniqueness compared with the lowland hill forest plots (Seamon et al. 2006).

TABLE 1

Species Ranked by Importance Value (IV), Listing Those Species in Each Plot with a Minimum IV of 10.0 (for All Plots, Species with IV Greater than 5.0 Are Listed)

| Coastal Plantation | | Coastal Forest | | Upper Plantation | | Upper Forest | | All Plots | |
|---|---|---|---|---|---|---|---|---|---|
| Species | IV | Species | IV | Species | IV | Species | IV | Species | IV |
| *D. samoense* | 64.2 | *D. samoense* | 117.6 | *A. altilis* | 72.1 | *H. tiliaceus* | 54.2 | *D. samoense* | 55.5 |
| *A. altilis* | 25.9 | *D. samoensis* | 15.8 | *D. samoense* | 62.5 | *S. inophylloides* | 26.2 | *A. altilis* | 28.6 |
| *M. harveyana* | 23.1 | *S. fanaiho* | 15.4 | *F. scabra* | 13.6 | *R. taitensis* | 20.4 | *H. tiliaceus* | 22.2 |
| *P. grandis* | 23.1 | *P. umbellifera* | 12.8 | *B. javanica* | 13.3 | *D. samoense* | 18.1 | *S. inophylloides* | 9.4 |
| *C. nucifera* | 21.8 | | | | | *A. zizyphoides* | 17.5 | *R. taitensis* | 8.7 |
| *H. nymphaeifolia* | 14.5 | | | | | *M. inutilis* | 16.7 | *A. zizyphoides* | 7.2 |
| | | | | | | | | *F. scabra* | 7.1 |
| | | | | | | | | *B. javanica* | 6.9 |
| | | | | | | | | *M. inutilis* | 6.9 |

## RESULTS

### *Forest Composition and Species Diversity*

In the total 6 ha, we encountered 54 tree species (Appendix). *Dysoxylum samoense* was the most abundant species across all four plots, followed by *A. altilis* and *H. tiliaceus* (Table 1).

A total of 18 species was found in the coastal plantation plot. This plot was heavily dominated by *D. samoense*, with *A. altilis*, *Macaranga harveyana*, *Pisonia grandis*, and *C. nucifera* of secondary importance (Table 1). There was one individual of *Crateva religiosa*. The coastal forest plot had 16 species and was dominated by *D. samoense*, followed by *Diospyros samoensis*, *Sterculia fanaiho*, and *Pisonia umbellifera* (Table 1). In the upper plantation, 26 tree species were recorded. This plot was dominated by *A. altilis* and *D. samoense*, with *Ficus scabra* and *Bischofia javanica* a distant third and fourth in importance (Table 1). There were 70 stems of *Morinda citrifolia*, several large *Spondias dulcis* trees, along with one *Carica papaya* stem and one *Syzygium malaccense* (Appendix). In the upper forest plot, a total of 35 species was encountered. *Hibiscus tiliaceus* was the most important species, followed by *Syzygium inophylloides*, *Rhus taitensis*, *D. samoense*, *Alphitonia zizyphoides*, and *Myristica inutilis* (Table 1). This plot also contained the species *Trichospermum richii*, *Pometia pinnata*, *Celtis harperi*, and *Litsea samoensis*, which are uncommon in American Samoa (*T. richii* is relatively more common than the other three species [E.L.W., pers. obs.]) and absent from the national park plots on Tutuila (Appendix; Webb and Fa'aumu 1999).

Several species exhibited wide variation in abundances across the plots (Appendix). Some of those differences were artifactual, such as *A. altilis* (a planted species), *Barringtonia asiatica* and *P. grandis* (coastal species), *C. nucifera* (a planted, coastal species), and *Hernandia nymphaeifolia* (a littoral species [Whistler 1992; J. Franklin, in an unpublished research report on the conservation of Tongan rain-forest biodiversity submitted to the Kingdom of Tonga, 2005] found in higher abundances in the coastal plantation because that plot was closer to the high-tide line than the coastal forest plot). However, other species exhibited abundance variation that reflected their ecologies; some of the distributions confirmed previous observations of the species, and some distributions may have provided new information of the species' ecologies (see Discussion).

Introduced (Polynesian or modern) species accounted for a significant proportion of the composition of the plantation plots (Appendix). Approximately 28% of all individuals and 26% of the basal area in the coastal plantation plot were nonnative, and 48% of the individuals and 40% of the basal area in the upper plantation were nonnative. The greatest contribution came from *A. altilis*, which

accounted for 13% and 40% of all individuals, and 13% and 32% of total basal area in the coastal plantation and the upper plantation plots, respectively. Two other important introduced species were *C. nucifera* and *M. citrifolia*. *Morinda citrifolia* has a naturalized, dispersed population in the forests of American Samoa, but *A. altilis* and *C. nucifera* generally are found only in agricultural areas. *Adenanthera pavonina* is by far the most aggressive invasive tree species we found in the plots, and it is speculated to be a threat to Samoan forests (Cronk and Fuller 2001). *Spondias dulcis*, planted in the upper plantation plot, had locally abundant seedlings. Although seedling regeneration appeared to be clumped near parent trees (E.L.W., pers. obs.), *S. dulcis* may be naturalizing on Ta'u.

Of particular interest was the finding of several nonnative *Flueggea flexuosa* individuals in the coastal plantation and upper forest plots (Appendix). To date there have been no formal reports of *F. flexuosa* escaping into natural forest in American Samoa. This is an important finding because it demonstrates that *F. flexuosa* may be naturalizing in forests of American Samoa.

Diversity indices revealed that in addition to the highest species richness, the upper forest plot was most diverse in terms of Simpson's $\lambda$. The modified Hill Ratio, which approaches zero as one species becomes increasingly dominant in the community, revealed that the species in the upper forest were the least evenly distributed. The cause for this result is that, besides the dominant species *H. tiliaceus* in the upper forest plot, only one other species, *M. inutilis*, had a relative abundance greater than 10.00. The relatively greater dominance of *H. tiliaceus* over species ranks 2, 3, and 4 than in other plots resulted in a lower evenness index.

Rarefaction curves revealed that the upper forest plot accumulated species at a faster rate than the other three plots and was similar to the forest plots on Tutuila (Figure 2). The two Ta'u plantation plots accumulated species at much lower rates than the Tutuila cultivation plot. In fact, the Alava plot accumulated species at the same rate as the other three less-disturbed Tutuila plots.

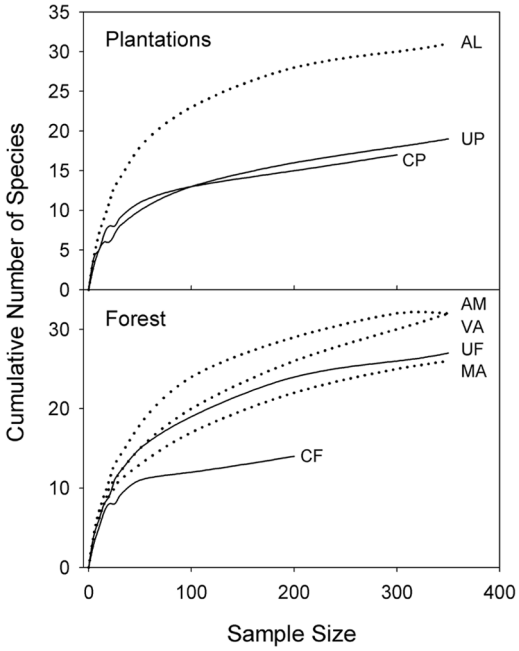


FIGURE 2. Rarefaction curves for the two plantation plots (upper panel: coastal plantation [CP], upper plantation [UP]) and the two forest plots (lower panel: coastal forest [CF], upper forest [UF]). Also graphed are rarefaction curves for four permanent plots on Tutuila: the regenerating plot Alava (AL) and three less-disturbed lowland forest plots, Amalau (AM), Maloata (MA), and Vatia (VA).

Morisita-Horn Indices revealed that high similarity existed between the coastal plantation and the coastal forest and between the coastal plantation and the upper plantation (Table 2). Moderate similarity existed between the coastal forest and the upper plantation, and low similarity was exhibited between the upper forest and any of the other three plots. The similarity values were heavily influenced by *D. samoense*. When *D. samoense* was removed from the plots, the recalculated Morisita-Horn Index dropped substantially for most comparisons, particularly between the coastal forest and the coastal plantation and between the coastal forest and the upper plantation (Table 2).

We used Morisita-Horn Indices to compare the Ta'u plots with forest data from Tutuila (Webb and Fa'aumu 1999, Seamon et al. 2006; E.L.W., unpubl. data). Of the four

TABLE 2

Morisita-Horn Index of Similarity across Four Plots on Ta'u, American Samoa, with Four Permanent Forest Plots on Tutuila (Webb and Fa'aumu 1999; E.L.W., Unpubl. Data) and with the Ottoville Lowland Forest (Seamon et al. 2006)

| | Coastal Plantation | Coastal Forest | | Upper Plantation | | Upper Forest | |
|---|---|---|---|---|---|---|---|
| Plot | | W | WO | W | WO | W | WO |
| Ta'u | | | | | | | |
| Coastal plantation | | 0.78 | 0.26 | 0.70 | 0.51 | 0.14 | 0.009 |
| Coastal forest | | | | 0.52 | 0.10 | 0.19 | 0.09 |
| Upper plantation | | | | | | 0.16 | 0.09 |
| Tutuila | | | | | | | |
| Alava (old plantation) | 0.02 | 0.06 | | 0.06 | | 0.65 | |
| Amalau | 0.08 | 0.14 | | 0.08 | | 0.47 | |
| Maloata | 0.02 | 0.12 | | 0.03 | | 0.45 | |
| Vatia | 0.02 | 0.12 | | 0.01 | | 0.26 | |
| Ottoville Lowland Forest | 0.38 | 0.23 | | 0.13 | | 0.06 | |

*Note:* Comparisons across Ta'u plots were made with all species included (W) and without *Dysoxylum samoense* (WO). Comparisons between Ta'u and Tutuila plots included all tree species.

Ta'u plots, the upper forest plot was the most similar to the lowland (hill) forest plots on Tutuila. The highest similarity was the Alava–upper forest pair, due in part to the fact that in both plots the two most abundant species were *Myristica inutilis* and *Hibiscus tiliaceus*. With those species removed from the analysis the similarity between Alava and the upper forest dropped to 0.45. The coastal plantation, coastal forest, and upper plantation had very low similarity values with the Tutuila plots, indicating uniqueness from the Tutuila plots. It is interesting that the upper forest plot, in which *Pometia pinnata* was found, had very low similarity with the Ottoville Lowland Forest, whereas the coastal plantation exhibited moderate similarity with the Ottoville Lowland Forest.

### *Forest Structure*

Forest structural parameters varied across the four plots. Tree densities ranged from 327 $ha^{-1}$ in the coastal forest to 633.5 $ha^{-1}$ in the upper forest, with the coastal and upper plantations intermediate (Appendix). Total basal areas ranged from 23.8 $m^2$ $ha^{-1}$ in the coastal plantation to 31.4 $m^2$ $ha^{-1}$ in the coastal forest. At the plot level and across the coastal plantation, upper plantation, and upper forest, plot stem density exhibited a marginally significant correlation with basal area ($n = 3$, Pearson $R = 0.992$, $P = .080$). The coastal forest, however, had the lowest tree density but the highest basal area as a result of that plot containing several massive *Dysoxylum* trees that accounted for 76.6% of the total plot basal area. Aggregated across all subplots, however, there was a highly significant positive correlation between stem density and basal area (partial correlation controlling for plot and elevation, $n = 600$, df = 596, Pearson $R = 0.89$, $P < .0001$).

Canopy height was 22.2 m in the coastal plantation, 28.5 m in the coastal forest, 16.6 m in the upper plantation, and 19.7 m in the upper forest (Kruskal-Wallis ANOVA, $n = 295$, chi-square = 203.6, df = 3, $P < .0001$). In the coastal plots, approximately half of all trees were less than 15 m height (55% coastal plantation, 50% coastal forest), whereas 86% of the stems in the upper plantation and 66% of the stems in the upper forest were less than 15 m height (Figure 3). Thirty-five percent of the stems in the coastal plantation were 15–19.9 m tall; therefore 90% of all stems in the coastal plantation, 98% of trees in the upper plantation, and 95% of the trees in the upper forest were less than 20 m tall. In contrast, 72% of the stems in the coastal forest were less than 20 m tall. To control for species effects on canopy height, we examined the dbh-height relationships for *D. samoense*, which was the

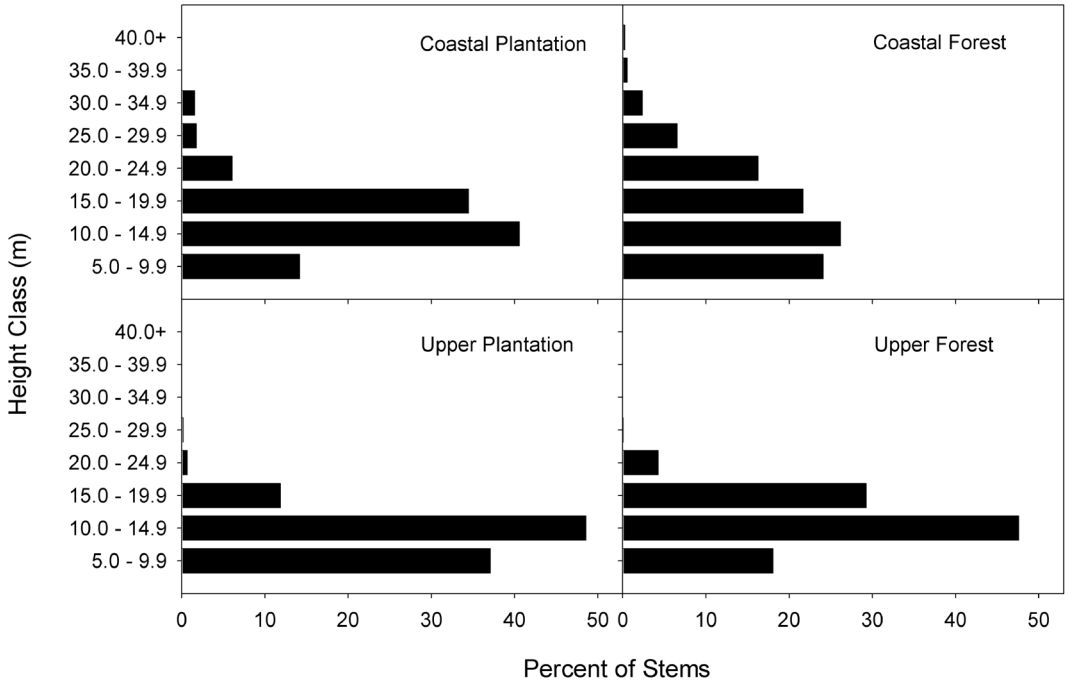


FIGURE 3. Tree height profiles in four permanent plots on Ta'u, American Samoa.

only species abundant in all four plots (Figure 4). Four *D. samoense* stems were greater than 20 m height in the two upper plots combined, whereas 26 stems in the coastal plantation and 69 stems in the coastal forest were at least 20 m tall. Moreover, within a diameter class, the median tree height was greater in the coastal plots than in their corresponding upper plots (Table 3). Thus, trees in the coastal plots were taller than those in their analogous upper plots, and in general trees in the forest plots were taller than those in their paired plantation plots.

The overall community diameter-class distributions showed that the proportional distribution of size classes was similar across sites, with the exception of the coastal forest plot where there was a higher proportion of large trees than in the other three plots (Figure 5). The basal area class distributions differed greatly across the four plots. In the coastal plantation, three basal area classes with the greatest contribution to overall basal area were 10–20 cm, 20–30 cm, and ≥100 cm dbh. In the coastal forest, 61% of the total basal area was contained in trees ≥60 cm dbh, in contrast to 34% in the coastal plantation, 7% in the upper plantation, and 6% in the upper forest. The upper plantation basal area distribution showed the greatest contribution to total basal area coming from trees 10–40 cm dbh and peaking in the 20–30 cm dbh class (about 35% total basal area in that class). The upper forest plot was similar to the upper plantation in that the three smallest size classes contributed the greatest to total community basal area, but the 10–20 cm dbh class contributed the most to basal area (about 27%).

There were clear differences in the size-class distributions for six important species in the two coastal plots (Figure 6). The only species that had similar size-class distributions in both coastal plots was *F. scabra*, but this is not surprising because it rarely achieves large dimensions (maximum dbh in the plots = 31.4 cm). Both *B. asiatica* and *D. samoense* had more regeneration (trees 10–20 cm dbh) but

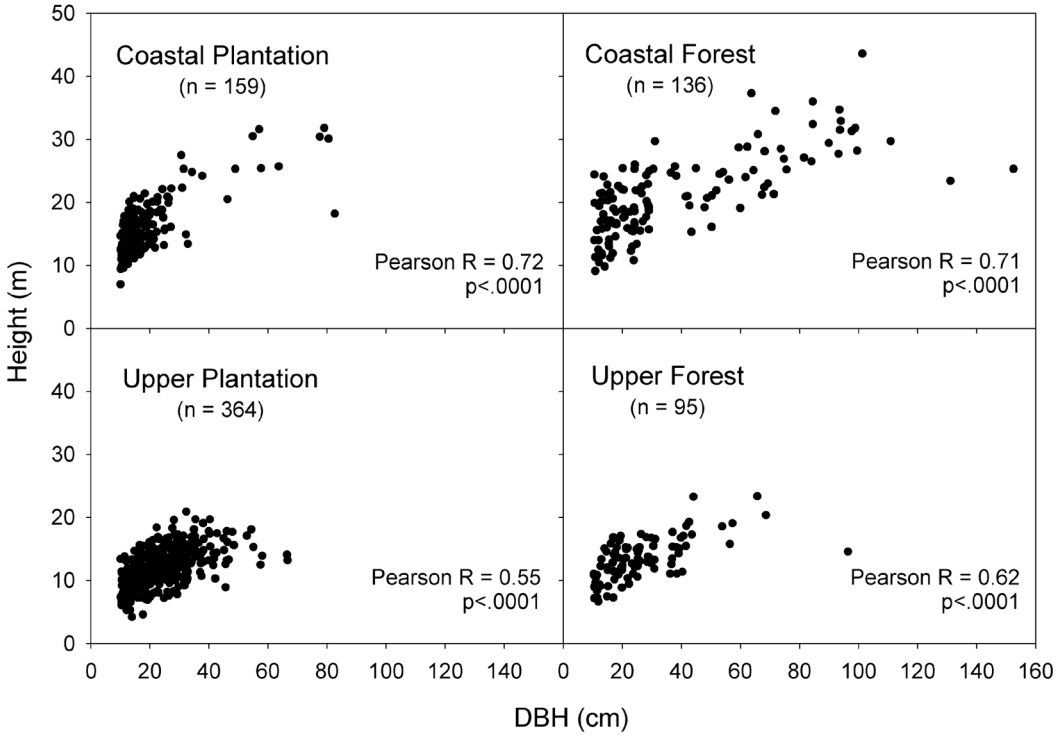


FIGURE 4. Scattergrams with correlations for diameter-height relationships of *Dysoxylum samoense* in four plots on Ta'u, American Samoa.

TABLE 3

Median Tree Height for *Dysoxylum samoense* in Each Diameter Size Class across Four Permanent Plots on Ta'u (Comparisons Were Not Made for Trees ≥60 cm dbh Due to Low Sample Sizes

| | Diameter Class (cm) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 10–19.9 | | 20–29.9 | | 30–39.9 | | 40–49.9 | | 50–59.9 | |
| Plot | *n* | Median Height | *n* | Median Height | *n* | Median Height | *n* | Median Height | *n* | Median Height |
| Coastal plantation | 116 | 15.1 | 26 | 17.0 | 7 | 24.2 | 2 | 22.9 | 3 | 30.5 |
| Coastal forest | 44 | 17.0 | 36 | 18.7 | 5 | 25.3 | 7 | 20.7 | 8 | 22.7 |
| Upper plantation | 149 | 10.1 | 124 | 12.8 | 65 | 13.9 | 19 | 14.8 | 5 | 15.3 |
| Upper forest | 41 | 11.1 | 27 | 13.5 | 14 | 14.7 | 7 | 17.3 | 3 | 18.6 |
| *P* value (Kruskal-Wallis ANOVA) | | <.001 | | <.001 | | <.001 | | <.005 | | <.005 |

had fewer trees ≥40 cm dbh in the coastal plantation plot than in the coastal forest. *Pisonia grandis* exhibited both greater regeneration and more large trees in the coastal plantation than in the coastal forest. In contrast, *D. samoensis* and *S. fanaiho* had higher numbers of trees in all size classes in the coastal forest plot than in the coastal plantation plot.

Comparison of tree size-class distributions

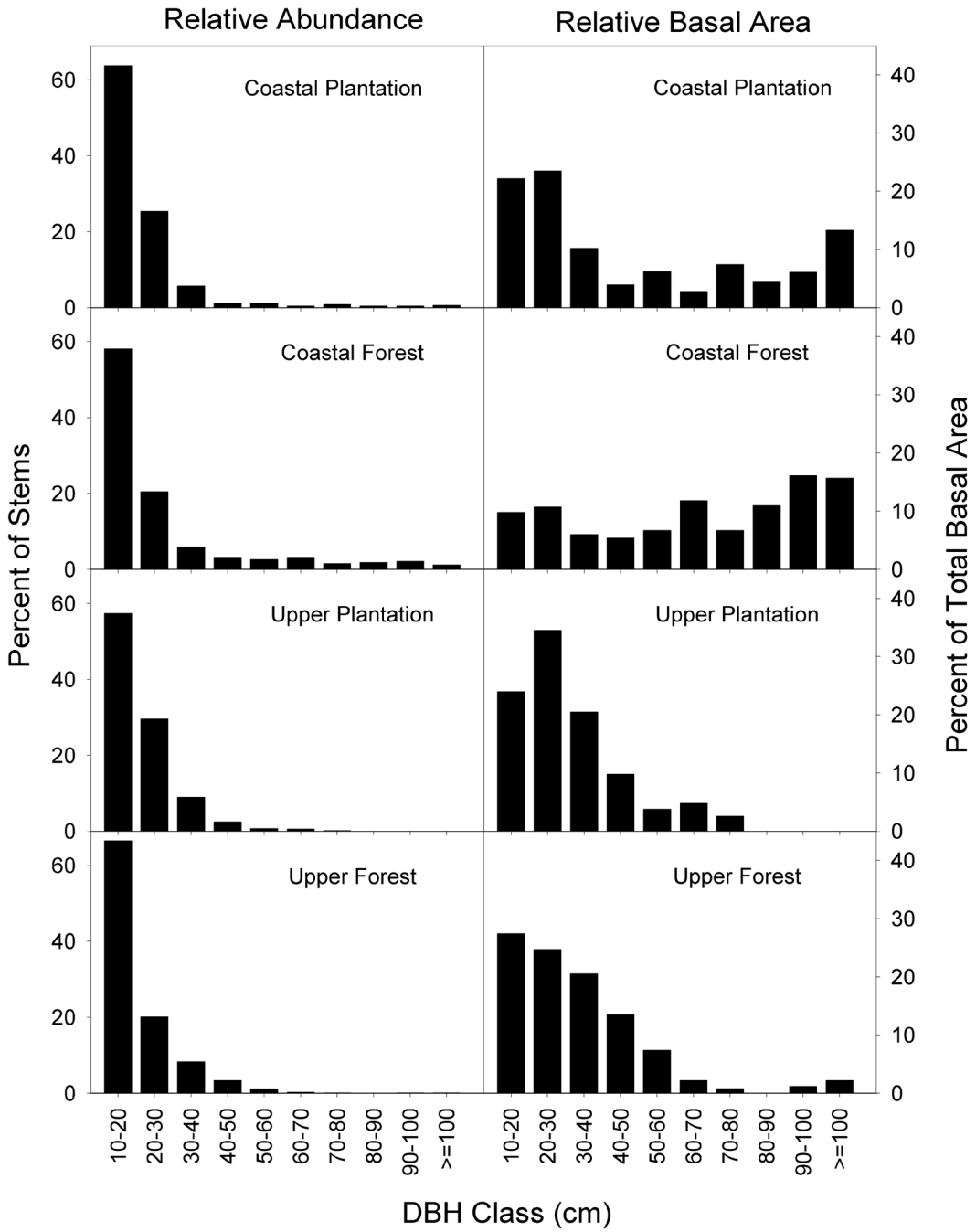


FIGURE 5. Tree community size-class distributions for the four plots on Ta'u, showing relative abundances per size class and the proportion of plot basal area contained in each dbh size class.

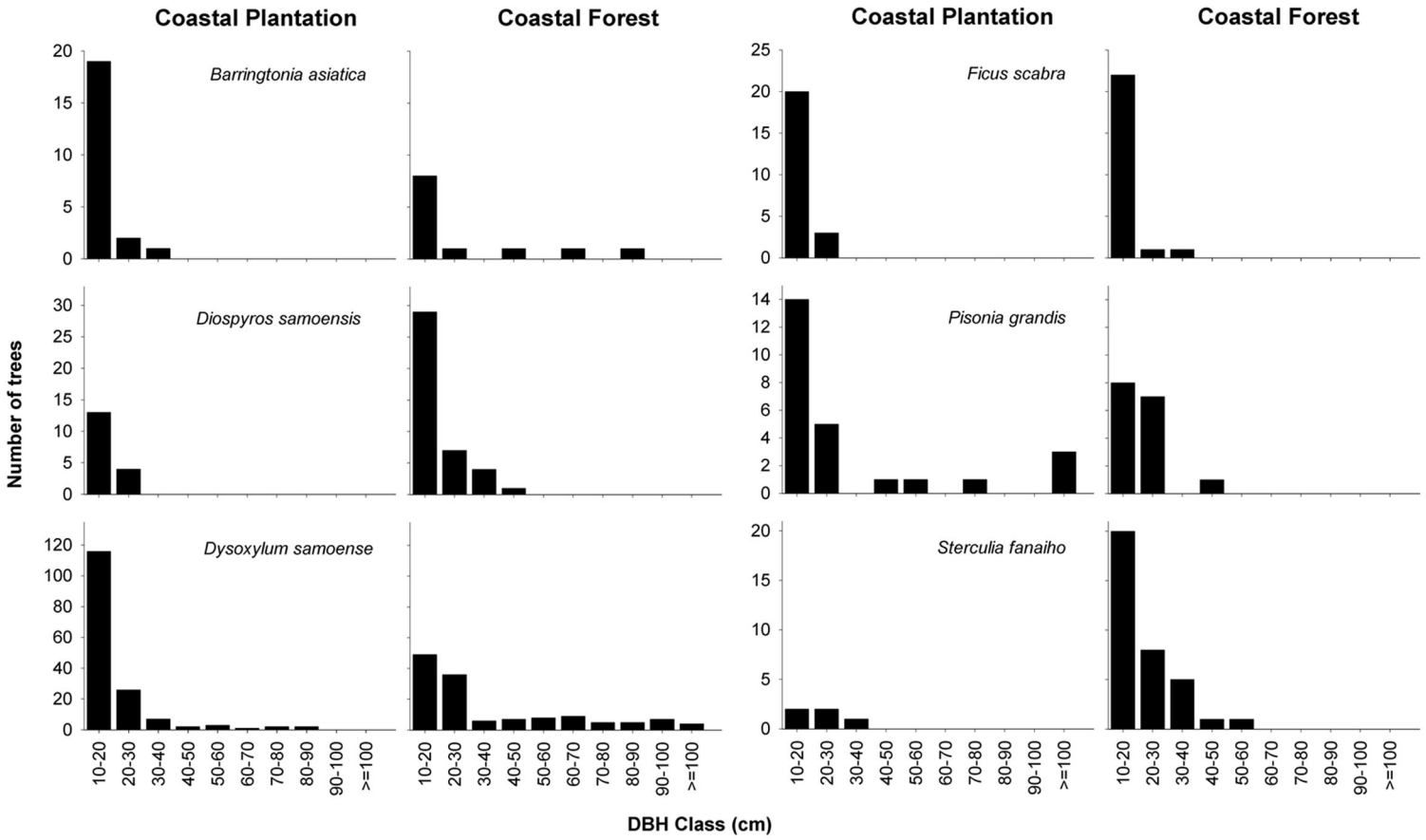


FIGURE 6. Size-class distributions for important species in the two coastal plots.

of important species between the upper plantation and the upper forest revealed that of eight species compared, five showed higher densities of trees in all size classes in the upper forest (Figure 7): *Alphitonia zizyphoides*, *H. tiliaceus*, *M. stipulosa*, *Rhus taitensis*, and *S. fanaiho*. A sixth species, *C. odorata*, had more trees of all size classes in the upper forest except for the 30–50 cm dbh classes. In contrast, *B. javanica* and *D. samoense* had more individuals (particularly the 10–20 cm dbh class) in the upper plantation than in the upper forest.

## DISCUSSION

According to rarefaction curves, the tree community richness of the upper forest plot on Ta'u is similar to that of the plots on Tutuila, 100 km to the west. However, the Morisita-Horn Index and the rarefaction curves revealed that the composition of the Ta'u upper forest plot was most similar to that of the Alava regenerating forest than to the other, later-successional, forests of Tutuila. The reason lies in the fact that the upper forest canopy was dominated by *S. inophylloides*, *R. taitensis*, *D. samoense*, and *A. zizyphoides*. *Rhus taitensis* and *A. zizyphoides* are considered to be dominant early-successional trees (Drake et al. 1996, Franklin et al. 1999), but *S. inophylloides* is a late-successional species. Thus, despite the lack of evidence for agricultural disturbance, this result confirmed earlier observations (Whistler 1992) that the forests along the eastern slope of Ta'u have been strongly impacted by disturbance and are in a state of succession. The presence of *S. inophylloides* indicates that if left undisturbed, the plot will mature into *Syzygium*-dominated mixed lowland forest (Whistler 1992). Increasing dominance of *S. inophylloides* in later-successional forests may be due to the dense wood of the species, which presumably allows it to persist in hurricane-disturbed forest relatively more successfully than other species (Whistler 1992, Webb et al. 1999). Over time, resistance of *S. inophylloides* to hurricanes, when other species would be uprooted, snapped, or severely damaged, would allow them to attain canopy stature and become an important canopy component. Recent data (E.L.W., unpubl. data) has revealed that *S. inophylloides* sustained less major damage (aggregated blowdowns and trunk snaps) than other tree species during cyclone Olaf in early 2005. Thus, the upper forest plot, having been less disturbed by human activity than the upper plantation plot, has had opportunities for late-successional or mature-phase species to establish and/or persist (i.e., *Aglaia samoensis*, *Calophyllum neo-ebudicum*, and *Canarium vitiense* [Webb and Fa'aumu 1999]). Given the fact that we made extensive reconnaissance hikes along the eastern slope in search of mature forest, and the upper forest plot represented what we agreed to be the most mature forest available, it is unlikely that any substantial stands of mature lowland (not coastal) forest, such as on Tutuila, can be found in the national park unit of Ta'u. However, long-term protection will provide ample opportunity for succession to occur within the natural disturbance regime.

The coastal plot we established included the 1,000-$m^2$ plot established by Whistler (1995), who recorded six species, 370 trees $ha^{-1}$, and 56.5 $m^2$ $ha^{-1}$. Six species among 37 trees is less than would be expected based on our derived rarefaction curve, but the tree density was similar. The largest difference between our results and those of Whistler (1995) is in terms of basal area, where our results are 56% of his. The difference is due to the fact that the smaller plot contained relatively more basal area in large trees. Moreover, *D. samoense* had a relative basal area of 76.6% in our 1.0-ha plot, but 93.3% in the smaller plot. Despite those differences, the five most important species in the larger coastal forest plot we established concur with those listed by Whistler (1995) as the most important.

Both coastal plots exhibited low diversity and low similarity with the upper plots (especially when *D. samoense* was removed from the similarity analysis) and virtually no similarity with any lowland hill plots on Tutuila. These two plots also showed low similarity with the Ottoville Lowland Forest on Tutuila, which is a *Dysoxylum*-dominated forest on very well-drained lava substrate. Thus,

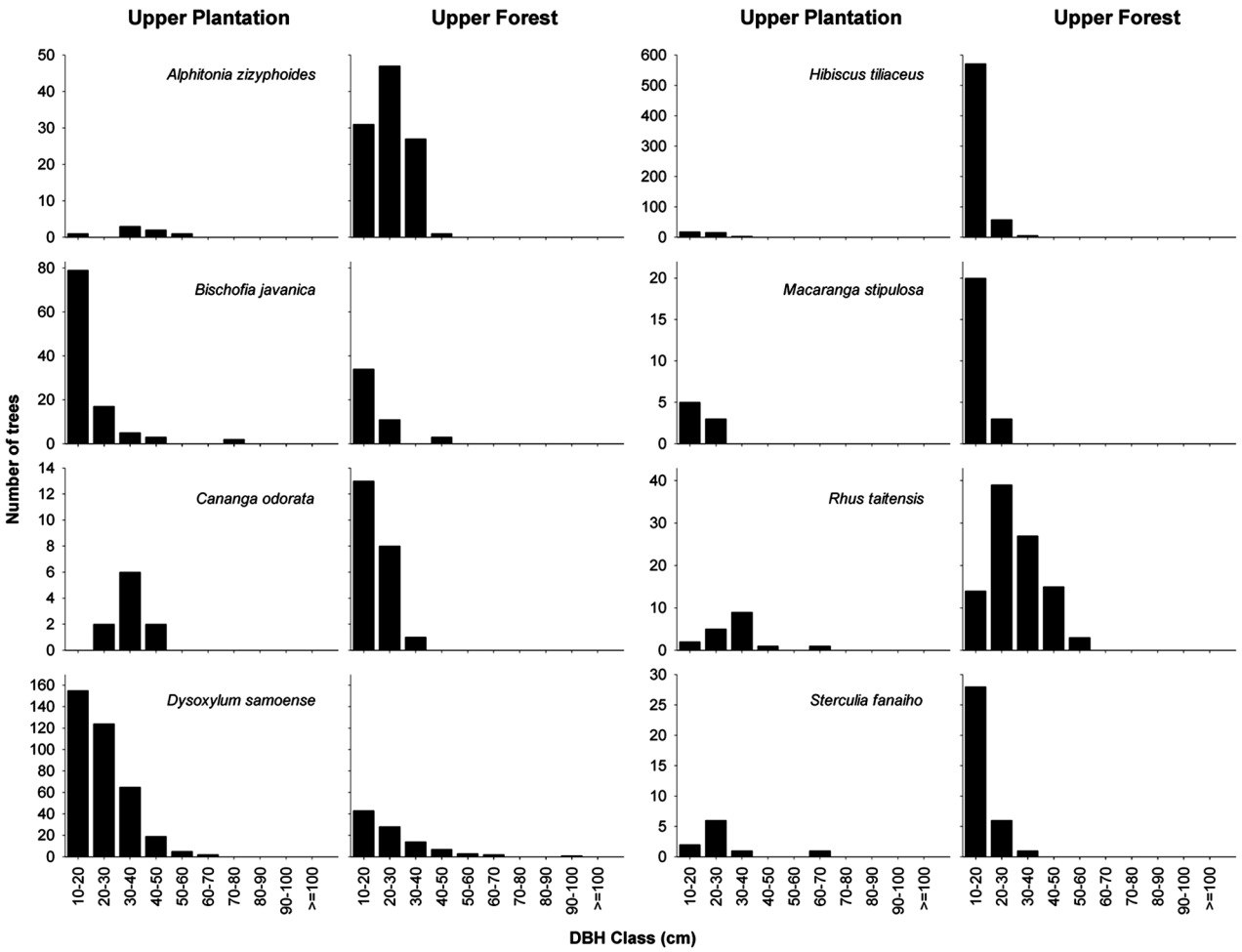


FIGURE 7. Size-class distributions for important species in the two upper plots.

the *Dysoxylum* coastal forest is indeed a unique habitat type, and as Whistler (1995) noted, it should be protected from human-induced disturbance.

Cyclones are an important factor in shaping forests of Samoa and Polynesia in general (Elmqvist et al. 1994, 2001, Hjerpe et al. 2001, Franklin et al. 2004). In addition to composition, canopy heights may be affected by hurricanes depending on the exposure of the plot. Overall canopy height was greater in the coastal forest plots than in their analogous upper plots, and this effect was seen at the species level, in *D. samoense*. This result indicates the effect of topography/elevation/exposure to canopy height in this study, which has been shown to be an important predictor of hurricane damage (Everham and Brokaw 1996). Webb et al. (1999) found significant differences in canopy height as a function of topography on Tutuila, with well-protected valley forests being significantly taller than exposed ridge forest. Topographical variability in terms of stream-dissected terrain is low on the eastern side of Ta'u. However, the escarpment between the coastal plots and the upper plots is an obvious topographical feature. This escarpment could affect the amount of damage sustained by forests during both chronic and catastrophic events. For example, in Fiji, 72% of the 50 recorded tropical storms (including cyclones) that passed within 180 nautical miles (333.4 km) of Lautoka (Viti Levu) came from the northwest (Brand 2003). Storm trajectory will affect both directionality and force of the winds striking a particular point. In the case of Ta'u it is possible that the coastal plots have been more protected from wind disturbance in the recent past than the upper plots.

Variability in composition and structure of the plots also reflects the agricultural histories we were able to ascertain from interviews. In the coastal plantation, nearly 25% of the relative abundance and relative basal area consisted of *A. altilis* and *C. nucifera*, and in the upper plantation *A. altilis* alone composed 40% of the relative abundance and 32% of the relative basal area. Prolific regeneration of *A. altilis*, which was evident during our field research, served to maintain dominance of this important agroforestry species in former plantations. Monitoring the two plantation plots will reveal the dynamics and compositional changes associated with succession in abandoned plantations (see also Franklin et al. 1999).

Successional development generally results in older forests having greater basal area than younger forests but not necessarily fewer stems (Aide et al. 1995, Guariguata and Ostertag 2001, Franklin 2003). In our study, basal area was greater in both forest plots than in their corresponding plantation plots. Stem density in the coastal plantation was greater than in the coastal forest plot, whereas the upper forest plot had greater stem densities than the upper plantation. The high stem densities in the plantations are due to the fact that trees such as *A. altilis* and *C. nucifera* were already present at the time of abandonment. Indeed, calculating total stem density and basal area in each plot without including those two species dramatically reduces those values. In the coastal plantation stem densities and basal area would be reduced to 348 trees $ha^{-1}$ and 18.2 $m^2$ $ha^{-1}$, respectively, and to 353 trees $ha^{-1}$ and 18.3 $m^2$ $ha^{-1}$ in the upper plantation.

Greater overall canopy heights in the forest plots than in their corresponding plantation plots may reflect the land management techniques of clearing large trees in heavily disturbed plantation areas. Large trees would be removed for plantations because the root systems and wide crowns would reduce agricultural output. Long-term monitoring of the compositional and structural changes of these forest plots will reveal the rate at which structural features change over time.

Several species had abundances across the plots that were notable because they may provide us with new information about the species' ecologies. First, *D. samoense* was found in high abundance in all plots and was a dominant or codominant species in three of the four plots. Although exhibiting the most prolific regeneration (dbh 10–20 cm) in the plantation plots, there was nevertheless regeneration of this species in the forest plots as well. Franklin (2003) classified *Dysoxylum*

*forsteri* in Tonga as a pioneer species (sensu Clark and Clark 1999). In contrast, Webb and Fa'aumu (1999) classified *D. maota* on Tutuila as a mature-phase species because it was nearly absent from their 1.2-ha regenerating cultivation plot. The fact that *D. samoense* was regenerating in both the coastal forest and the upper forest plots is evidence that this species is a generalist that prefers disturbed sites. This agrees with the observations made by Whistler (1980:112) that *D. samoense* is "able to establish itself in disturbed places, but persists and even dominates when other signs of disturbances are gone."

*Hibiscus tiliaceus* exhibited the highest densities in the upper forest plot, but since abandonment approximately 17 yr earlier only a few *H. tiliaceus* individuals successfully established in the upper plantation and attained large size. We interpret this to mean that *H. tiliaceus* may require a long time to establish a robust population in disturbed forest, but that when established it is able to persist (i.e., a persistent successional species sensu Webb and Fa'aumu 1999).

The high abundances of *Macaranga harveyana* and *Morinda citrifolia* in the coastal and upper plantations agree with earlier observations that these species achieve maximum abundances in disturbed forest (Hjerpe et al. 2001, Nelson 2005). The fruits of these species are highly favored by Samoan starlings (*Aplonis atrifusca* [Whistler 2004; J. Seamon, Department of Marine and Wildlife Resources, Government of American Samoa, pers. comm.]), which can be found across a variety of forest habitats but tend to be found in more disturbed or nonnative habitat (Friefeld 1999). Thus, rapid dispersal into the abandoned plantations, or the existence of a dormant seed bank, permitted relatively large populations of *M. harveyana* and *M. citrifolia* to establish rapidly. The low abundance of *M. harveyana* in the upper plantation, despite having a known elevation range up to 400 m (Whistler 1992), is consistent with its low densities in upland hill forest of Tutuila (Webb and Fa'aumu 1999, Webb et al. 1999) and may indicate a preference of this species for well-drained, coastal soils rather than upland soils.

*Pisonia umbellifera* exhibited a stem density of 33 $ha^{-1}$ in the coastal forest plot but was completely absent from the coastal plantation plot. Because it is a small tree, all the individuals of this species would have been removed before planting crop species (similarly, removal of the small tree species *Barringtonia samoensis* probably occurred in the upper plantation site as well, but its presence in the upper plantation plot can largely be explained by a tight cluster of 14 trees within an ca. 400-$m^2$ block at the south edge of the plot that may have escaped cultivation). The complete absence of *P. umbellifera* individuals $\geq$10 cm dbh in the coastal plantation plot is probably the result of this species requiring a long time to regenerate after disturbance and/or requiring intact forest to regenerate. Seamon et al. (2006) found strong edge effects on *P. umbellifera* in the Ottoville Lowland Forest, indicating that human-related disturbances may negatively impact the persistence of this species. Whether limited regeneration in the coastal plantation plot is a function of low dispersal rates or certain germination/growth requirements is not clear, and further research on this species is needed. In either case, we interpret this pattern to mean that *P. umbellifera* is a mid-successional, and perhaps a late successional, species.

The presence of *Pometia pinnata* in the upper forest plot, albeit in low densities (5.5 trees $ha^{-1}$), suggests that there are conditions on Ta'u favorable to the establishment of this species. According to Whistler (1980), "Tava lowland forest" dominated by *P. pinnata* is exclusively found on soils underlain with lava. As a shield volcano, much of Ta'u was formed through basaltic magma eruptions followed by slow lava flows that laid down a substratum of lava, upon which soil formation occurred. Pavaiai soils up to about 275–300 m elevation above the escarpment therefore provide an adequate substrate for *P. pinnata* to establish and persist. The coastal Ngedebus substrate not being underlain with lava was the likely reason that *P. pinnata* was not present in the coastal forest plots. During our reconnaissance hikes we also found *P. pinnata* on the southern plateau of Ta'u (Li'u

Bench), which is also covered with Pavaiai series soil. So *P. pinnata* should be relatively widespread and in low densities on lowland Ta'u up to about 275 m. Nevertheless, the low similarity of 0.06 between the upper forest and the Ottoville Lowland Forest clearly indicates that the Ta'u forest where *P. pinnata* is found is completely distinct from the Ottoville Lowland Forest. Thus, Seamon et al.'s (2006) conclusion that the Ottoville Lowland Forest is a unique forest formation in American Samoa and worthy of conservation is supported by our findings.

The higher abundances of trees and regeneration of *Sterculia fanaiho* in the forest plots than in the plantation plots were notable. The Sterculiaceae are often found in open or disturbed forests. Higher abundances of *S. fanaiho* in the coastal plantation than in the coastal forest suggest that it is either a "persistent successional" or a "generalist" species (sensu Webb and Fa'aumu 1999).

*Trichospermum richii* was only found in the upper forest plot. Because this species has only been reported above 100 m elevation (Whistler 1992, 1994), we did not expect to find it in the coastal plots. There have been no studies on the ecology of this species, so the regeneration requirements are not known. Our interpretation of some previous botanical surveys (Kirkpatrick and Hassall 1981, 1985, Keppel et al. 2005) is that it may be found principally in unmodified forest, but Whistler (2004) described it as common in disturbed foothill and montane forest. *Trichospermum richii* appears to be more common on Ta'u than on Tutuila (Webb and Fa'aumu 1999, Webb et al. 1999). Research on the population dynamics and regeneration requirements of this species would be useful.

Our assumption when interpreting differential abundances and size-class distributions is that the results reflect either the impact of disturbance (human or environmental) or the specific ecological features of the species. However, it should also be recognized that pathogens may play a role in the spatial distributions of the tree species. Brooks (2002) found spatially explicit patterns of infection of *Phellinus noxius* (Corner) Cunningham in forests of Tutuila. Infection rates were highest in forests disturbed by humans and most prevalent in the species *M. fatua*, *D. samoense*, and *H. tiliaceus*. Therefore, although we did not record whether *P. noxius* was present in the Ta'u plots, we cannot disregard it as a potential, yet unquantified, mortality vector influencing the representation and spatial patterns of trees in these plots.

Introduced species have become a common feature in the forests of American Samoa, but as yet they are not as threatening to native biodiversity as is the case in other island systems (e.g., Meyer and Florence 1996). Although 99% of all nonnative individuals in this study were species considered not to be a major threat to native species of American Samoa, monitoring and proactive action must take place. For example, we documented several mature *Flueggea flexuosa* trees in both coastal and upland forest on Ta'u. This species has been widely promoted as a potentially valuable tree in American Samoa for use as building material. The fruits of *F. flexuosa* are favored by several species of birds, including purple-capped fruit doves (*Ptilinopus porphyraceus*) and Pacific pigeons (*Ducula pacifica*) (J. Seamon, Department of Marine and Wildlife Resources, unpubl. data). Therefore, although it is not surprising that *F. flexuosa* escaped into natural forest, it is important to recognize it as a potentially invasive species. Other tree species in American Samoa have been introduced only to naturalize and become aggressive invasives, notably *Adenanthera pavonina*, *Castilla elastica* Cerv., and *Paraserianthes falcataria* (L.) I. Neilsen, the latter of which has been the focus of an intensive eradication program within the National Park of American Samoa. As of yet, there have been no reports of *P. falcataria* on Ta'u, but *C. elastica* has already arrived (E.L.W., pers. obs.). We recommend that *F. flexuosa* be included in the list of potential invasive species for American Samoa. The plots for this study will give a small sample size of trees to estimate growth rates and possibly localized regeneration, but more thorough studies of the growth and regeneration of *F. flexuosa* in native forest of American Samoa are necessary to determine the level of threat posed by this species.

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## Appendix 1

Summary Information for Four Plots on Ta'u, American Samoa

| Species | Status[a] | Coastal Plantation (1 ha) | | | | Coastal Forest (1 ha) | | | | Upper Plantation (2 ha) | | | | Upper Forest (2 ha) | | | | All Plots (6 ha) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | NO/HA | RA | BA/HA | RBA | NO/HA | RA | BA/HA | RBA | NO/HA | RA | BA/HA | RBA | NO/HA | RA | BA/HA | RBA | NO | RA | BA | RBA |
| *Adenanthera pavonina* L. | MI | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 0.5 | 0.08 | 0.03 | 0.10 | 0.5 | 0.08 | 0.01 | 0.03 | 2 | 0.06 | 0.07 | 0.04 |
| *Aglaia samoensis* A. Gray | E | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 1.5 | 0.24 | 0.02 | 0.06 | 3 | 0.09 | 0.03 | 0.02 |
| *Alphitonia zizyphoides* (Spreng.) A. Gray | I | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 3.5 | 0.59 | 0.44 | 1.62 | 51.5 | 8.13 | 2.73 | 9.34 | 110 | 3.41 | 6.35 | 3.78 |
| *Artocarpus altilis* (Parkinson) Fosberg | PI | 61 | 13.29 | 2.99 | 12.56 | 0 | 0.00 | 0.00 | 0.00 | 233.5 | 39.68 | 8.82 | 32.41 | 0 | 0.00 | 0.00 | 0.00 | 528 | 16.35 | 20.63 | 12.27 |
| *Barringtonia asiatica* (L.) Kurz | I | 15 | 3.27 | 0.54 | 2.26 | 10 | 3.06 | 1.31 | 4.16 | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 25 | 0.77 | 1.85 | 1.10 |
| *Barringtonia samoensis* A. Gray | I | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 8.5 | 1.44 | 0.11 | 0.42 | 0 | 0.00 | 0.00 | 0.00 | 17 | 0.53 | 0.23 | 0.14 |
| *Bischofia javanica* Bl. | I | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 36.5 | 6.20 | 1.94 | 7.11 | 23 | 3.63 | 0.80 | 2.73 | 119 | 3.68 | 5.47 | 3.25 |
| *Calophyllum inophyllum* L. | I | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 0.5 | 0.08 | 0.63 | 2.15 | 1 | 0.03 | 1.26 | 0.75 |
| *Calophyllum neo-ebudicum* Guillaumin | I | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 1 | 0.16 | 0.01 | 0.04 | 2 | 0.06 | 0.02 | 0.01 |
| *Cananga odorata* (Lam.) Hook. f. Thoms. | PI | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 5 | 0.85 | 0.46 | 1.68 | 11 | 1.74 | 0.33 | 1.13 | 32 | 0.99 | 1.57 | 0.94 |
| *Canarium vitiense* A. Gray | I | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 1 | 0.16 | 0.08 | 0.27 | 2 | 0.06 | 0.16 | 0.09 |
| *Carica papaya* L. | MI | 1 | 0.22 | 0.01 | 0.06 | 0 | 0.00 | 0.00 | 0.00 | 0.5 | 0.08 | 0.01 | 0.02 | 0 | 0.00 | 0.00 | 0.00 | 2 | 0.06 | 0.02 | 0.01 |
| *Celtis harperi* Horne | I | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 1 | 0.16 | 0.03 | 0.12 | 2 | 0.06 | 0.07 | 0.04 |
| *Cerbera manghas* L. | I | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 3 | 0.47 | 0.12 | 0.42 | 6 | 0.19 | 0.25 | 0.15 |
| *Cocos nucifera* L.[b] | PI (I) | 50 | 10.89 | 2.59 | 10.91 | 0 | 0.00 | 0.00 | 0.00 | 2 | 0.34 | 0.14 | 0.51 | 0 | 0.00 | 0.00 | 0.00 | 54 | 1.67 | 2.87 | 1.71 |
| *Crataeva religiosa* Forst. f. | I | 1 | 0.22 | 0.02 | 0.08 | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 1 | 0.03 | 0.02 | 0.01 |
| *Diospyros samoensis* A. Gray | I | 17 | 3.70 | 0.33 | 1.38 | 39 | 11.93 | 1.22 | 3.89 | 0 | 0.00 | 0.00 | 0.00 | 1.5 | 0.24 | 0.02 | 0.07 | 59 | 1.83 | 1.59 | 0.95 |
| *Dysoxylum samoense* A. Gray | I | 157 | 34.20 | 7.13 | 29.98 | 134 | 40.98 | 24.06 | 76.58 | 157.5 | 26.76 | 9.72 | 35.71 | 42 | 6.63 | 3.37 | 11.50 | 690 | 21.36 | 57.37 | 34.11 |
| *Elattostachys falcata* (A. Gray) Radlk. | I | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 5.5 | 0.87 | 0.14 | 0.47 | 11 | 0.34 | 0.27 | 0.16 |
| *Elaeocarpus floridanus* Hemsl. | I | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 17.5 | 2.76 | 0.33 | 1.14 | 35 | 1.08 | 0.67 | 0.40 |
| *Erythrina variegata* L. | I | 0 | 0.00 | 0.00 | 0.00 | 2 | 0.61 | 0.08 | 0.27 | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 2 | 0.06 | 0.08 | 0.05 |
| *Euodia hortensis* Forst. | PI | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 0.5 | 0.08 | 0.01 | 0.02 | 1 | 0.03 | 0.01 | 0.01 |
| *Ficus obliqua* Forst. f. | I | 2 | 0.44 | 0.03 | 0.12 | 1 | 0.31 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 3 | 0.09 | 0.03 | 0.02 |

| | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Ficus scabra* Forst. f. | I | 23 | 5.01 | 0.41 | 1.72 | 24 | 7.34 | 0.40 | 1.28 | 54 | 9.18 | 1.21 | 4.44 | 4.5 | 0.71 | 0.05 | 0.16 | 164 | 5.08 | 3.32 | 1.98 |
| *Ficus tinctoria* Forst. f. | I | 0 | 0.00 | 0.00 | 0.00 | 1 | 0.31 | 0.02 | 0.07 | 0.5 | 0.08 | 0.00 | 0.01 | 1 | 0.16 | 0.01 | 0.04 | 4 | 0.12 | 0.05 | 0.03 |
| *Flacourtia rukam* Zoll. & Mor. ex Mor. | I | 0 | 0.00 | 0.00 | 0.00 | 1 | 0.31 | 0.02 | 0.05 | 0 | 0.00 | 0.00 | 0.00 | 15 | 2.37 | 0.26 | 0.89 | 31 | 0.96 | 0.53 | 0.32 |
| *Flueggea flexuosa* Muell. Arg. | MI | 9 | 1.96 | 0.31 | 1.32 | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 4.5 | 0.71 | 0.10 | 0.35 | 18 | 0.56 | 0.52 | 0.31 |
| *Garuga floribunda* Decne. | I | 2 | 0.44 | 0.04 | 0.16 | 8 | 2.45 | 0.53 | 1.69 | 4 | 0.68 | 0.56 | 2.07 | 0 | 0.00 | 0.00 | 0.00 | 18 | 0.56 | 1.70 | 1.01 |
| *Glochidion ramiflorum* Forst. | I | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 2 | 0.34 | 0.08 | 0.31 | 0 | 0.00 | 0.00 | 0.00 | 4 | 0.12 | 0.17 | 0.10 |
| *Hernandia nymphaeifolia* (Presl.) Kub. | I | 10 | 2.18 | 2.93 | 12.32 | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 10 | 0.31 | 2.93 | 1.74 |
| *Hibiscus tiliaceus* L. | I | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 17 | 2.89 | 0.67 | 2.46 | 216.5 | 34.18 | 5.86 | 20.02 | 467 | 14.46 | 13.06 | 7.77 |
| *Inocarpus fagifer* (Park.) Fosb. | PI | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 0.5 | 0.08 | 0.01 | 0.02 | 1 | 0.03 | 0.01 | 0.01 |
| *Litsea samoensis* (Christoph.) A. C. Smith | I | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 1 | 0.16 | 0.05 | 0.18 | 2 | 0.06 | 0.11 | 0.06 |
| *Macaranga harveyana* Muell. Arg. | I | 76 | 16.56 | 1.56 | 6.56 | 3 | 0.92 | 0.07 | 0.21 | 0.5 | 0.08 | 0.01 | 0.02 | 0 | 0.00 | 0.00 | 0.00 | 80 | 2.48 | 1.64 | 0.97 |
| *Macaranga stipulosa* Muell. Arg. | E | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 1.5 | 0.25 | 0.12 | 0.44 | 11 | 1.74 | 0.21 | 0.71 | 25 | 0.77 | 0.66 | 0.39 |
| *Meryta macrophylla* (Rich) Seem. | I | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 1 | 0.16 | 0.01 | 0.04 | 2 | 0.06 | 0.02 | 0.01 |
| *Morinda citrifolia* L. | PI | 7 | 1.53 | 0.23 | 0.97 | 9 | 2.75 | 0.13 | 0.41 | 35 | 5.95 | 0.51 | 1.87 | 2 | 0.32 | 0.03 | 0.10 | 90 | 2.79 | 1.44 | 0.85 |
| *Myristica inutilis* Rich ex A. Gray | I | 0 | 0.00 | 0.00 | 0.00 | 11 | 3.36 | 0.34 | 1.08 | 1.5 | 0.25 | 0.01 | 0.05 | 64 | 10.10 | 1.92 | 6.56 | 142 | 4.40 | 4.21 | 2.50 |
| *Neonauclea forsteri* (Seem. ex Havil) Merr. | I | 1 | 0.22 | 0.00 | 0.00 | 2 | 0.61 | 0.11 | 0.34 | 0.5 | 0.08 | 0.06 | 0.21 | 15.5 | 2.45 | 0.48 | 1.63 | 35 | 1.08 | 1.17 | 0.70 |
| *Omalanthus nutans* (Forst.) Guillemin | I | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 0.5 | 0.08 | 0.01 | 0.02 | 0 | 0.00 | 0.00 | 0.00 | 1 | 0.03 | 0.01 | 0.01 |
| *Pipturus argenteus* (Forst. f.) Wedd. | I | 3 | 0.65 | 0.03 | 0.13 | 0 | 0.00 | 0.00 | 0.00 | 9 | 1.53 | 0.15 | 0.54 | 0 | 0.00 | 0.00 | 0.00 | 21 | 0.65 | 0.32 | 0.19 |
| *Pisonia grandis* R. Br. | I | 21 | 4.58 | 4.41 | 18.54 | 16 | 4.89 | 0.62 | 1.97 | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 37 | 1.15 | 5.03 | 2.99 |
| *Pisonia umbellifera* (Forst.) Seem. | I | 0 | 0.00 | 0.00 | 0.00 | 33 | 10.09 | 0.85 | 2.71 | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 33 | 1.02 | 0.85 | 0.51 |
| *Planchonella garberi* Christoph. | I | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 6 | 0.95 | 0.68 | 2.33 | 12 | 0.37 | 1.37 | 0.81 |
| *Pometia pinnata* Forst. | I | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 5.5 | 0.87 | 0.30 | 1.01 | 11 | 0.34 | 0.59 | 0.35 |
| *Psydrax merrillii* (Setchell) Whistler | I | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 3 | 0.47 | 0.07 | 0.23 | 6 | 0.19 | 0.13 | 0.08 |
| *Rhus taitensis* Guillemin | I | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 5.5 | 0.93 | 0.83 | 3.03 | 44.5 | 7.02 | 3.92 | 13.38 | 100 | 3.10 | 9.49 | 5.64 |
| *Spondias dulcis* Forst. | MI | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 3.5 | 0.59 | 0.98 | 3.61 | 0 | 0.00 | 0.00 | 0.00 | 7 | 0.22 | 1.97 | 1.17 |
| *Sterculia fanaibo* Setchell | I | 3 | 0.65 | 0.22 | 0.92 | 33 | 10.09 | 1.67 | 5.30 | 5 | 0.85 | 0.34 | 1.25 | 17.5 | 2.76 | 0.37 | 1.27 | 81 | 2.51 | 3.31 | 1.97 |

**Appendix 1** (continued)

| Species | Status[a] | Coastal Plantation (1 ha) | | | | Coastal Forest (1 ha) | | | | Upper Plantation (2 ha) | | | | Upper Forest (2 ha) | | | | All Plots (6 ha) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | NO/HA | RA | BA/HA | RBA | NO/HA | RA | BA/HA | RBA | NO/HA | RA | BA/HA | RBA | NO/HA | RA | BA/HA | RBA | NO | RA | BA | RBA |
| *Syzygium malaccense* Merr. & Perry | MI | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 0.5 | 0.08 | 0.01 | 0.03 | 0 | 0.00 | 0.00 | 0.00 | 1 | 0.03 | 0.02 | 0.01 |
| *Syzygium inophylloides* (A. Gray) C. Muell. | I | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 47 | 7.42 | 5.49 | 18.74 | 94 | 2.91 | 10.97 | 6.52 |
| *Syzygium samarangense* (Bl.) Merr. & L. M. Perry | MI | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 2 | 0.32 | 0.03 | 0.10 | 4 | 0.12 | 0.06 | 0.03 |
| *Trema cannabina* Lour. | I | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 0.5 | 0.08 | 0.01 | 0.04 | 0 | 0.00 | 0.00 | 0.00 | 1 | 0.03 | 0.02 | 0.01 |
| *Trichospermum richii* (A. Gray) Seem. | I | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.00 | 10.5 | 1.66 | 0.81 | 2.77 | 21 | 0.65 | 1.62 | 0.96 |
| Sum | | 459 | | 23.78 | | 327 | | 31.42 | | 588.5 | | 27.23 | | 633.5 | | 29.27 | | 3230 | | 168.20 | |
| Number of species | | 18 | | | | 16 | | | | 26 | | | | 35 | | | | 54 | | | |
| Simpson's $\lambda$ | | 0.18 | | | | 0.21 | | | | 0.25 | | | | 0.15 | | | | | | | |
| Modified Hill evenness ratio | | 0.65 | | | | 0.59 | | | | 0.58 | | | | 0.51 | | | | | | | |
| Canopy height[c] | | 23.9 (±4.0) | | | | 29.4 (±4.3) | | | | 17.2 (±2.1) | | | | 20.3 (±1.7) | | | | | | | |
| Number of introduced species | | 5 | | | | 1 | | | | 8 | | | | 7 | | | | 12 | | | |
| Percentage of species introduced | | 27.8 | | | | 6.3 | | | | 30.8 | | | | 20 | | | | 22.2 | | | |
| Percentage of all individuals being introduced species | | 27.9 | | | | 2.8 | | | | 47.7 | | | | 3.3 | | | | 22.9 | | | |
| Percentage of total basal area coming from introduced species | | 25.8 | | | | 0.4 | | | | 40.2 | | | | 1.8 | | | | 17.4 | | | |

*Note:* NO/HA, the number of individuals per hectare; RA, relative abundance; BA/HA, basal area per hectare of all stems; RBA, relative basal area of all stems. GPS points for the NE corner of each plot using the UTM coordinate system (datum NAD83) are as follows: coastal plantation: E 670209, N 8424413; coastal forest: E 670251, N 8424663; upper plantation: E 669970, N 8425889; upper forest: E 669857, N 8425231.

[a] E, endemic; I, indigenous; PI, a Polynesian introduction; MI, a modern introduction. Status of the species is according to Whistler (1992, 1994; pers. comm.).

[b] *Cocos nucifera*, although probably indigenous (Whistler 1994), is considered as a Polynesian introduction for this paper because it was planted in the plots.

[c] The average height of the top 10% of all trees in the plot (see text).